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Salicylic Acid: A Versatile Signaling Molecule in Plants

M. Iqbal. R. Khan[1] · Peter Poor[2] · Tibor Janda[3]

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This special issue of *Journal of Plant Growth Regulation* (JPGR) provides an excellent platform and opportunity to publish authentic and novel research as well as review papers relative to salicylic acid. Numerous authors have succeeded in the elucidation of salicylic acid-mediated alleviation of both abiotic and biotic stresses. Additionally, the authors have also focused on in-depth understanding of plant growth and development responses modulated by salicylic acid. Altogether, the underlined research topic as presented here provides a brief appraisal on the recent advancement in salicylic acid biology research. The present issue will ascertain the problem from a fundamental framework to applied scientific knowledge-based queries and/or uncertainties, which needed to be addressed and driven by plant biologists and researchers towards the common future goal through optimizing the current research topic.

Salicylic acid and its derivatives, collectively referred to as salicylates are endogenously produced signaling molecules that activate plant defense responses against both abiotic and biotic stresses. Before salicylic acid was identified as an important plant signaling molecule, it was thought to be a minor byproduct along with many other phenolic secondary metabolites. However, progressively increasing studies relative to salicylic acid biology research indicated that it plays an important role, not only in regulating plant disease resistance, but also in regulating abiotic stress tolerance such as thermo-regulation, providing protection against oxidative stress-induced damages, and thus influences different aspects of the plant life cycle. Conclusively, salicylic acid arbitrates: (1) the accretion of osmolytes, which can aid in the safeguarding of osmotic homeostasis, (2) modulating mineral nutrition uptake, (3) increased scavenging capacity of reactive oxygen species (ROS), (4) enhanced accumulation of secondary metabolites and their production such as terpenes, phenolics, and nitrogen-containing compounds (alkaloids, cyanogenic glucosides, and non-protein amino acids), and sulfur-containing compounds (glutathione, glucosinolates, phytoalexins, thionins, and defensins), and (5) induction of other phytohormone biosynthesis pathways (Khan et al. 2015; Rasheed et al. 2020). Depending on the concentration range used, a plethora of studies indicated has confirmed the ameliorative functions of salicylic acid including plant growth induction and development in response to different abiotic and biotic stresses. The current special issue contains original research papers and review articles that explain salicylic acid's regulatory role in plant development, and how it interacts with biotic and abiotic stress factors. It also evaluated the relevant literature and illuminated the major prospects. To facilitate finding the respective topics of the articles in this issue, the papers have been divided into two groups.

Salicylic Acid Regulates Plant Abiotic Stress Responses

Plants are being continuously exposed to prevalent abiotic stresses including salt, drought, temperature, flooding, and heavy metal stress due to challenging environmental conditions. Considering these adverse scenarios, the application of salicylic acid was found beneficial in modulating morpho-physiological and biochemical responses, along with yield-related attributes under various abiotic stresses. Stress factors trigger transcriptional and metabolic changes in plants, in which RNAi is associated with gene expression regulation at the post-transcriptional level and with chromatin modification in transcriptional silencing. Balassa et al. (2022) found that exogenous salicylic acid treatment results in an expression pattern similar to that of provoked by drought stress in several RNAi genes. They suggested that salicylic acid could induce a priming mechanism through RNA-dependent DNA

✉ M. Iqbal. R. Khan
iqbal.khan@jamiahamdard.ac.in

[1] Department of Botany, Jamia Hamdard, New Delhi, India

[2] Department of Plant Biology, University of Szeged, Szeged, Hungary

[3] Department of Plant Physiology, Agricultural Institute Centre for Agricultural Research, Martonvásár, Hungary

methylation and chromatin remodeling, which may result in the faster activation of stress-responsive metabolic routes, such as anthocyanin biosynthesis.

The application of salicylic acid with seed-priming method has emerged as one of the most reliable and cost-effective approach in mitigating abiotic stresses. For instance, Ahmad et al. (2020) reported that seed-priming with salicylic acid in pea (*Pisum sativum*) resulted in increase in overall plant performance such as growth and photosynthesis-related attributes, induced antioxidant defense system comprising superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX) and glutathione reductase (GR), and increased accumulation of osmotic-regulators including soluble sugars and proline. Similarly, Kaur et al. (2022) also examined the effects of salicylic acid by seed-priming or pre-soaking method in chickpea (*Cicer arientum*) under salt stress. The results revealed that salicylic acid treatment has retained plant biomass, photosynthetic efficiency, arrested nodule senescence, and diminished oxidative stress via up-regulated stimulation of ROS-quenching machinery leading to restored productivity and yield in salt-stressed chickpea plants. Moreover, Hayat et al. also gave information on salicylic acid-mediated salt tolerance mechanisms, and reported that salicylic acid promoted the orchestration of innate immune system-mediated responses in giant juncao (*Pennisetum giganteum*) under salt stress. Furthermore, salicylic acid counteracted salt stress-induced damages by regulating osmolyte assimilation accompanied with ionic homeostasis with lowered chlorogenic acid production, which in turn increased plant growth, tolerance indices, influenced biochemical parameters such as photosynthetic pigments and protein content (Hayat et al. 2022). In another study, Jannesar et al. (2022) showed that salicylic acid treatment in pistachio (*Pistacia vera*) under salt stress enhanced the photosynthetic pigments, antioxidant enzymatic activities of SOD, CAT, POX, and polyphenol oxidase (PPO), which were reflected with reduced accumulation of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2). Rasheed et al. also examined the effect of salicylic acid on mustard under salt stress, and reported improved photosynthetic activity, sulfur assimilation, enzymatic as well as non-enzymatic antioxidants, which led to reduced ROS concentration (Rasheed et al. 2021). These responses further aided in imparting salt tolerance in mustard plants.

Singh et al. (2022) showed the significant effect of plant growth regulators (PGRs) including salicylic acid on rice (*Oryza sativa*) under salt stress, and found that salicylic acid treatment triggered a multitude number of physiological responses such as photosynthesis rate, and minimizes the accumulation of oxidative stress indicators, which further led to increased agronomic attributes and improved crop productivity. In addition to salt stress, temperature fluctuations also possess detrimental effects on plant physiology, and implications of salicylic acid under such conditions have been evaluated. For instance, Yang et al. documented salicylic acid treatment in rice under heat stress based on physiological characteristics, spikelet differentiation, yield, and grain quality (Yang et al. 2021). They observed that SOD, POX, and CAT antioxidant activities were enhanced, with increased concentrations of osmotic regulators including proline and soluble sugars. These responses were coherent with decreased MDA content found and leaf temperature under high-temperature condition, leading to increased rice production and grain yield quality. Additionally, Basirat and Mousavi showed positive regulation of nutritional and yield status in salicylic acid treated cucumber (*Cucumis sativus*) under high temperature, and thus mitigated the adverse impacts by facilitating nutrient management under such conditions (Basirat and Mousavi 2022). As a part of heat stress, the thermal fluctuations are becoming more frequent and severe in various countries that are threatened by climate change. Ihsan et al. (2022) investigated the effects of plant growth regulators, such as salicylic acid under high day/night temperatures (34/30 °C, 38/34 °C, and 42/38 °C) in *Triticum aestivum*. The high temperature significantly reduced plant growth and grain setting, and 100-grain weight. At the same time, they found that the application of salicylic acid along with methyl jasmonate resulted in significant improvements in grain filling and grain protein content under high-temperature stress by the regulation of the activity of photosynthesis and antioxidant enzymes such as SOD.

The effects of and role of salicylic acid in responses to cold stress have been studied for a long time (Janda et al. 1999). Wang et al. elucidated the significant role of salicylic acid in wheat (*Triticum aestivum*) under freezing stress, and found that sucrose and free proline concentration reduced cell death with coordinated carbon and nitrogen metabolism, and thus aided in conferring tolerance against freezing stress (Wang et al. 2021). Furthermore, Duan et al. (2022) also showed that salicylic acid could improve the frost tolerance of *Magnolia wufengensis*. They also demonstrated that in parallel with increasing amylase, sucrose-P-synthase and sucrose synthase activities, salicylic acid promoted the accumulation of soluble sugars, including glucose, fructose, and raffinose. Their results suggested that changes in sugars metabolism may also be part of salicylic acid-induced stress tolerance.

Under the present era of vigorously changing environments, the plant faces simultaneous abiotic stresses rather than single stress. Considering this, Dawood et al. examined the effect of salicylic acid under concurrent stress (drought and salinity) in two cultivars of *Vicia faba* (Assuit wardy and Assuit 84). The results demonstrated by Dawood et al. (2021) revealed that salicylic acid improved growth traits, restores photosynthetic pigments, maintained water-relations, modulated mineral nutrients in the root-shoot system by restricting the influx of sodium (Na^+) and potassium (K^+) ions, and boosted accumulation of osmotic-regulators. Additionally, salicylic acid treatment energizes antioxidant capacity, which was coherent with the minimal accumulation of oxidative stress biomarkers such as lipoxygenase (LOX) activity. Salicylic acid-induced salt tolerance may also related to increasing nutrient uptake, and essential oil production (Ghassemi-Golezani and Farhadi 2021). Furthermore, the study conducted by Iqbal et al. (2022) for examining the effect of salicylic acid in mustard (*Brassica juncea*) under water deficit and low nitrogen supply conditions showed an increase in nitrogen use efficiency (NUE), water use efficiency (WUE), and photosynthesis-related processes such as stomatal conductance and intercellular carbon dioxide (CO_2) concentration.

There are numerous studies conducted in recent years emphasizing on the interactive as well as the reproductive link between salicylic acid and other phytohormones such as auxin, ethylene (ET), abscisic acid (ABA), gibberellic acid (GA), jasmonic acid (JA), and cytokinins (CKs) for inducing abiotic stress tolerance in plants. However, only a few studies deciphered the crosstalk between the salicylic acid and other phytohormones under different abiotic stresses. For instance, Iqbal et al. (2022) showed that salicylic acid application influenced the biosynthesis of ABA as well as ethylene (ET) in mustard under water deficit or drought stress and limited supply of nitrogen. In another study, Rasheed et al. (2021) found that ET interceded with the effect of salicylic acid in the presence of sulfate ions (SO_4^{2-}) which enhanced antioxidant capacity leading to sulfur assimilation in salt-stressed mustard plants. The results from the aforementioned studies indicated the potential interactive role between salicylic acid and other phytohormones in mitigating abiotic stress-induced adversities in plants, and thus aided in achieving sustainable goal of crop production.

Salicylic Acid Regulates Defensive Genes Expressions

Defensive genes play a crucial role in eliciting several physiological as well as molecular responses, and aid in alleviating abiotic stress in plants. There are numerous studies targeting the role of abiotic stress-induced defensive gene expressions have been well-studied and elucidated in the literature. For instance, Ahmad et al. reported that salicylic acid significantly alleviated salt stress-induced ionic toxicity by the up-regulation of Na^+/H^+ antiporters including *SALT OVERLY SENSITIVE 1* (*SOS1*) and *Na^+/H^+ exchanger* (*NHX1*) in pea plants. The activation of these transports induces Na^+ efflux from cytosol and sequester in vacuoles leading to salt-stress tolerance (Ahmad et al. 2020). Additionally, a study conducted by Jannesar et al. (2022) showed that salicylic acid positively regulated isochorismate synthase (*ICS*) gene expressions, which is a rate-limiting enzyme in the salicylic acid biosynthesis pathway, leading to salt-stress tolerance in pistachio plants.

Author Contributions All the authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

Declarations

Conflict of interest The authors declare that the work was conducted in the absence of any commercial or financial relationships that could be constructed as a potential conflict of interest.

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